VARIABILITY IN OAT STEM RUST IN EASTERN AUSTRALIA

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Synopsis

An unexpected degree of variability in *P. graminis* f. sp. *avenae* was revealed when isolates from eastern Australia were tested on the International Differential Set. Of the genes present in the differential set only *pg-8* provided a comprehensive protection against the pathogen.

Four grass stem rust cultures including one of *P. graminis lolii* were found to be related to oat stem rust. Certain selected genotypes from *Avena ludoviciana* and *A. fatua* were susceptible to all these cultures except to one of *P. graminis dactylidis*. Other single plant progenies from *A. ludoviciana* differentiated between the cultures.

Introduction

Although about two million acres are sown annually to oats in N.S.W., none of the currently recommended cultivars having resistance to oat stem rust, incited by *Puccinia graminis* Pers. f. sp. *avenae* Eriks. and E. Henn., were bred in Australia. The cultivar Garry introduced from Canada, carries two factors conditioning stem rust resistance but is susceptible to some field strains. Cultivar Saia, which belongs to the diploid sand oat species *Avena strigosa* Schreb., was introduced from Brazil and is grown for green feed production in Queensland and northern N.S.W. It is resistant to most strains of oat stem rust. Recently, breeding programmes have been initiated to incorporate stem rust resistance into commercial varieties, and the present studies were carried out to determine pathogenic variability in the oat stem rust fungus in eastern Australia.

Review of Literature

In 1923 Stakman, Levine and Bailey differentiated oat stem rust races on three cultivars, and Bailey (1925) published an analytical key based on reactions on these genotypes: White Tartar (gene D=*Pg–1*), Richland (gene A=*Pg–2*) and Joanette Strain (gene E=*Pg–3*). For about thirty years oat stem rust investigators utilized these three monogenic varieties (or their equivalents) for identifying races. However, with the release of cultivars with the Hajira (or "Canadian") type of resistance (gene B=*Pg–4*) in North America, strains of stem rust virulent on plants with this resistance became widespread. Later, oat rust workers used two recessive genes to subdivide oat stem rust races. Green and Samborski (1962) used a line of Eagle^2 × C.I. 4023 with the gene F (*pg–8*) and Green (1965) reported that Santa Fe Selection C.I. 5844 with the gene H (*pg–9*) was useful as a differential variety. Earlier Stewart *et al.* (1956) had found a culture which attacked Saia, and since then this diploid has been used as a supplemental tester in North America. From 1957 cultures were designated on the basis of their behaviour on the original three testers and supplemental differentials, with alphabetical suffixes, often confusingly applied, were used. To overcome inherent difficulties associated with this procedure, Stewart and Roberts (1970) proposed the adoption of a standard international differential set comprising the above seven testers. "New race" numbers were assigned beginning with race 14, leaving races 1–13, described on the original three testers,

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unchanged. They also supplied an analytical key for these seven testers and presented the infection types of 97 new race numbers together with their virulence/avirulence indices. Recently genes for resistance other than those present in the above seven testers have been studied, *viz.*, *pg–11* (McKenzie and Martens, 1968), *pg–12* (Martens *et al.*, 1968) and *pg–13* (Roelfs and Rothman, 1971). The last gene has come into usage as a differential in the U.S.A., but the three genes have not been incorporated into the international set.

Waterhouse (1952) reviewed the work on oat stem rust variability in Australia until 1951. Using the three differentials White Tartar, Richland and Joanette Strain, he distinguished six physiologic races, *viz.*, 1, 2, 3, 6, 7 and 8. Of these, races 1 and 2, and 3 and 7, could be separated only at low temperatures on Joanette, and consequently, for rust survey purposes race 1 was grouped with race 2, and race 3 with race 7. The former were avirulent on plants with gene *Pg–1*, while races 3 and 7 attacked those with this gene.

During the years 1928 to 1938, 706 collections were tested, of which 85·7 per cent were race 1 and/or 2, 12·6 per cent were race 3 and/or 7, 0·4 per cent were race 8, which is virulent on plants with *Pg–2* and *Pg–3*, and 1·3 per cent belonged to race 6, which attacks all three genes *Pg–1*, *Pg–2* and *Pg–3*. This shows the prevalence of race 1 and/or 2 in the early years ; for example, during the first three seasons (1925–1927) only these types were recovered.

Of the 901 collections from all states of Australia and 30 collections from New Zealand studied by Waterhouse from 1939 to 1951, 57 per cent were identified as belonging to races 1 and/or 2. In each state they accounted for the majority of rust samples. Thirty-five per cent of the isolates proved to be race 3 and/or 7. and the remaining 8 per cent were race 8. Thus a significant shift towards virulence on *Pg–1* had taken place in the Australian oat stem rust flora during these two periods.

About 30 per cent (278) of the collections made by Waterhouse came from grasses, mainly *Avena fatua* L., *Lamarckia aurea* (L.) Moench., *Hordeum leporinum* Link., *Avena sterilis* L., *Dactylis glomerata* L. and *Amphibromus neesii* Steud. The percentages of the three abovementioned physiologic types based on these 278 isolates were 60, 34 and 6 respectively ; thus they did not significantly differ from collections made on commercial oats.

Materials and Methods

Field collections of oat stem rust were tested annually during the last two seasons (1970–1971, 1971–1972) and a high proportion of samples from wild oats were included.

All isolates were observed on a set of 12 stocks which comprised : (1) seven differentials identical with the seven differential hosts used by Stewart and Roberts (1970) or substitutes carrying the same major gene, *viz.*, White Tartar 05* (*Pg–1*=gene D), Richland 08 (*Pg–2*=gene A), Joanette Strain R.L. 561 0617 (*Pg–3*=gene E), Rodney 0654 (*Pg–4*=gene B), Eagle^2×C.I. 4023 0658 (*pg–8*= gene F), Santa Fe Reselection C.I. 5844–1 0661 (*pg–9*=gene H) and Saia C.I. 7010 0589 ; (2) two testers which possess the same major gene present in two varieties of group (1), *viz.*, Sevnothree C.I. 3251 0255 (*Pg–3*) and Rosen's Mutant C.I. 8159 0659 (*pg–9*) ; (3) two testers which combine major genes, *viz.*, Garry R.L. 1692 0605 (*Pg–2*, *Pg–4*) and Minn. A.G. 331 0615 (*Pg–1*, *Pg–2*) ; and (4) C.I. 3034 0660 which carries *Pg–1* and *pg–11*. Notes were recorded after 14 days on seedlings maintained at temperatures ranging from 15° C to 21° C. Infection types and nomenclature follow those of Stewart and Roberts (1970).

In addition to the field isolates, four cultures of grass stem rust, *viz.*, 69013 (*P. graminis* f. sp. *lolii* Guyot and Massenot), 69177 (tentatively designated

* 0 numbers refer to the Sydney University Oat Accession Register.

TABLE 1

Infection Types Produced on Eight International Testers by 22 Strains of P. graminis avenae

Strain		Testers of Group 1							Supplementary Tester C.I. 3034 *Pg-1 pg-11*	New Race No.*
Virulence Index	Accession Number	White Tartar *Pg-1*	Richland *Pg-2*	Joanette Strain *Pg-3*	Rodney *Pg-4*	Eagle[2] × C.I. 4023 *pg-8*	Sante Fe Reselection *pg-9*	Saia Undesig.		
0	71077	2	1+	;1‡	1	2	2	0;	2	1
0	70535	2	1+	X+	1	2	2	0;	2	5
1	70538	3+	1+	;1‡	1	2	2	0;	2	3, 49
1	71502	3+	1+	;1‡	2+	2	2	;	2	3
1, 11	R3	3+	1+	X+	1	2	2	0;	3+	
2	71577	2	3+	;1‡	1	2	2	0;1	2	11
2	BC3	2	3+	X+	1	2	2	0;	2	10
3	BC1	2	1+	3+	1	2	2	0;	2	2
1, 2	70388	3+	3+	;1‡	1	2	2	0;	2	
1, 3	BC2	3+	1+	3+	1	2	2	0;	2	7
1, 3, 11	R7	3+	1+	3+	1	2	2	X	3+	
1, 4	70553	3+	1+	X+	3+	2	2	0;	2	25
1, Sa	70590	3+	1+	X+	1	2	2	3+	2	
2, 3	70611	2	3+	3+	1	2	2	0;	2	8
2, 4	BC59	2	3+	X+	3+	2	2	0;	2	23
2, 9	R10	2	3+	X+	1	2	3	0;	2	82
3, 9	R2	2	1+	3+	1	2	3	X=	2	77
9, Sa	71394	2	1+	X+	1	2	3+	3+	2	
1, 2, 3	70497	3+	3+	3+	1	2	2	0;	2	6
2, 3, 4	70553	2	3+	3+	3+	2	3−	0;	2	22
2, 3, Sa	70590	2	3+	3+	1	2	3−	3+	2	
2, 3, 9, Sa	68001	2	3+	3+	1	2	3+	3+	2	

* According to Stewart and Roberts (1970).

P. graminis f. sp. *dactylidis* Guyot and Massenot), 69243 and 69968 which were found on *Deyeuxia quadriseta* Benth. and *Phalaris* sp., respectively were studied. All four cultures were described by Luig and Watson (1972).

Experimental Results

(*a*) *Oat stem rust*

Using six testers with different single genes for resistance and Saia as proposed by Stewart and Roberts (1970), the Australian cultures can be differentiated into 22 strains on the basis of their reaction spectra (Table 1). Certain strains with the same virulence index were not considered identical. For instance, strain 1 (70538) and strain 1 (71502) are discriminated on the basis of their low and intermediate infection types respectively, on plants with *Pg–4*. Two of the strains are characterized by a virulent reaction on *pg–11* present in C.I. 3034.

Table 2
Percentages of Total Isolates of Oat Stem Rust Avirulent on Single Genes for Resistance in the Seasons 1970–1971 and 1971–1972

Gene	1970–71	1971–72
Pg–1	55·8	88·1
Pg–2	53·2	66·2
Pg–3	80·6	85·7
Pg–4	78·8	85·9
pg–8	100·0	100·0
pg–9	86·3	94·7
Saia	94·1	94·9

This degree of variability was unexpected as resistant cultivars carrying these genes have not been grown. Moreover, strains virulent on plants with these genes were quite widespread during the last two seasons 1970–1971 and 1971–1972 (Table 2). On the other hand acreages sown to the Canadian cultivar Garry and to Saia are too small to give the more virulent strains a definite advantage. By contrast little variation was encountered with wheat stem rust, *P. graminis* f. sp. *tritici* Eriks. and E. Henn., during the period 1929–1941 (Waterhouse, 1952) when the bulk of the inoculum in all Australian states comprised a single strain and nearly all wheat cultivars were susceptible.

No cultures virulent on plants with *pg–8* (gene F) were found, indicating that in Australia the gene present in C.I. 8111 (Eagle)^2 × (Hajira × Joanette) is the best source of resistance among the genes present in the differentials.

On Joanette Strain (*Pg–3*), Rodney (*Pg–4*) and Saia, two resistant infection types were recorded (Table 1). It is possible that Saia possesses more than a single gene for resistance since Murphy *et al.* (1958) found two independent dominant genes for resistance in another *strigosa* variety, C.D. 3820. However, Rodney apparently possesses only a single gene for resistance. The variation on Rodney could be due to multiple alleles for virulence in the pathogen. Watson and Luig (1968) have described progressive increases in infection types on varieties with single genes for resistance in the case of wheat stem rust. On Joanette Strain clearly two levels of resistance were exhibited, and the variety Sevnothree which carries the same gene *Pg–3*, reacted similarly to all strains shown in Table 1. The resistant infection types on both varieties are very temperature-sensitive, high temperatures resulting in susceptibility.

Two of the strains listed in Table 1 produced susceptible infection types on the tester C.I. 3034 which possesses the genes *Pg–1* and *pg–11*. Since the bulk of the inoculum and the majority of the strains are avirulent on *Pg–1*, it

is not possible to assess the extent of virulence on *pg–11* in the oat stem rust flora, but it seems certain that this partially recessive gene is of limited value for breeding. Resistance at the *pg–11* locus appears to be closely associated with yellow-green plant colour, but there is no close linkage between *pg–11* and the genes *Pg–2*, *Pg–3* and *Pg–4* (McKenzie and Martens, 1968). Thus *pg–11* could be combined with one or more of these factors.

A large proportion of the samples collected from wild oats and from other wild and cultivated grasses yielded more than one strain, including strains with several genes for virulence. This agrees with the findings of Roelfs and Rothman (1971), who reported that the patterns of the oat stem rust isolates in the U.S.A. differed according to the hosts from which the collections were made. They found that race 61 (7F) accounted for 2 per cent of the isolates obtained from commercial oats, but was identified in 29 and 18 per cent of the isolates examined from barley and wild grasses (mainly *A. fatua*) respectively. The fact that Waterhouse (1952) observed no differences in race patterns when collections made from cultivated and wild oats were compared may have been due to the few resistance genes used in the differential set at that time.

(*b*) *Related Grass Rusts*

When the four stem rust cultures which are pathogenic on grass species but which cannot attack cultivars of wheat, oats or rye (Luig and Watson, 1972) were inoculated on seedlings of 12 selected oat varieties, the resulting high infection types suggested that some of them must be considered closely related to *P. graminis avenae* (Table 3). However, the very low infection types produced by the cultures on the 12 differentials of the Australian oat stem rust set (Table 4), as compared to those induced by an avirulent strain of *P. graminis avenae*, indicate that they are different from oat stem rust.

TABLE 3

Infection Types Produced by a Strain of Oat Stem Rust and Four Grass Stem Rusts on 12 Selected Oat Varieties

	Variety		Stem Rust Culture				
W Number	Varietal Name	Botanical Name	Strain 3 *P. gr. avenae*	69968	69243	69013 *P. gr. lolii*	69177 *P. gr. dactylidis*
09	Algerian	*A. sterilis*	3+	3=	1‡3=	0;1	0
026	Short Oat	*A. brevis*	3+	3+	3+	2+3	:1+
028	Wild Oat	*A. sterilis polystachya*	3+	;1	;1, 1‡	X−	0
033	Yarran	*A. sativa*	3, 3+	;	;1‡	;1, 2	0
054	Fulghum	*A. sativa*	3+	X, 2‡	2+3	0	0
0128	Bond	*A. sativa*	3+	;1‡	22+	23−	0
0132	Kendall	*A. sativa*	3+	3c3	2‡3−	X	0
0175	Belar	*A. byzantina*	3+	X−, X	1‡, 23−	X−	0
0182	Glabrota	*A. strigosa*	3+	33+	33+	23−	2=2−
0202	C.I. 3498	*A. strigosa*	3+	2−2+	33+	2+3−	0;
0210	Bond × Iogold	*A. sativa*	2=2−	2−2	;1=	23−	0
0335	Erban	*A. sativa*	3+	2+3	2+3−	2	;1=

Luig and Watson (1972) suggested that two of the cultures, *viz.* 69243 and 69968, could be of hybrid origin. The high infection types produced by 69013 (*P. graminis lolii*) on the 12 selected oats, however, were unexpected, as this *forma specialis* was believed to be a true grass rust which had specialized on genotypes of *Lolium* sp. (Waterhouse, 1951). The fourth culture (69177) showed little virulence on all oat varieties tested, but it is highly pathogenic on most genotypes of *Dactylis glomerata*.

TABLE 4

Infection Types Produced by an Avirulent Strain of Oat Stem Rust and Four Grass Stem Rusts on the 12 Australian Oat Stem Rust Testers

	Genes Involved		*P. gr. avenae* 71622	Grass Stem Rusts			
	Alphab. Desig.	Pg Desig.	Strain 0	69968	69243	69013	69177
Richland 08	A	*Pg–2*	1+	;	;	;	0
Rodney 0654	B	*Pg–4*	1+	;1	0	0	0
White Tartar 05 ..	D	*Pg–1*	2–	;	0	0	0
Jostrain 0617	E	*Pg–3*	1+	;1=	0;	0	0
Eagle[2] × C.I. 4023 0658 ..	F	*pg–8*	2–	;1	;1	;1=	0
Santa Fe Reselection 0661	H	*pg–9*	X+	0;	0	0	0
Saia 0589	Undesig.	Undesig.	0;	3	X	2	0
Minnesota A.G.331 0615..	A, D	*Pg1 Pg2*	1+	0	0	0;	0
Garry 0605	A, B	*Pg2 Pg4*	1+	0;	0	0	0
C.I. 3034 0660	A–	*Pg–1 pg–11*	1+2–	;1	;1=	0	0
Rosen's Mutant 0659 ..	H	*pg–9*	1+2	;1	;1=	0	0
Sevenothree 0255 ..	E	*Pg–3*	1+	3	2+	0	0

(*c*) *Stem Rust on Wild Oats*

Waterhouse (1952) demonstrated that in Australia oat stem rust survives well on native and introduced grasses, and that species of wild oats are the most common hosts. The aim of the present work with wild oats, initiated by Professor I. A. Watson, was to detect a genotype susceptible to many strains of *P. graminis avenae* and related rusts. Such a genotype could then be utilized

(i) as a susceptible medium for somatic hybridization studies between these rusts,

(ii) as a susceptible parent in crosses with resistant genotypes to determine the genetic basis of resistance to the avirulent cultures used in this study, and

(iii) as a recurrent parent for transferring individual genes for resistance into a susceptible background. Such genes could comprise the recognized *Pg* series, and also genes for resistance to the avirulent cultures. Data from pathogenic studies, some of which are presented in Table 3, suggest that there exist, previously unrecognized, many genes for resistance to these cultures.

A large number of single plant progenies from common wild oats (*Avena fatua*) and winter wild oats (*A. ludoviciana* Durieu) were tested with the four grass rusts. All were resistant to culture 69177 and to strains of wheat stem rust and rye stem rust, *P. graminis* f. sp. *secalis* Eriks. and E. Henn., but with the other three rusts variability was apparent (Table 5).

TABLE 5

Infection Types Produced on Single Plant Progenies of Wild Oats by Cultures of P. graminis

Wild Oat Selection	Grass Rusts				*P. gr. avenae*
	69968	69243	69013	69177	Strain 1, 9
A. ludoviciana A1	3+	3c	3c	0;	3+
„ „ B	3+	;	X+	0	3+
„ „ F	3+	3+	0;	0	3+
„ „ L	;1=	;1=	0;	0	3+
A. fatua A	;1=	;	0	0	3+
„ „ WOA ..	3+	3+	3+	0	3+

Certain genotypes of *A. ludoviciana* (B and F) were resistant when tested with cultures 69243 and 69013, while giving susceptible reactions to 69968. Again, other genotypes of *A. ludoviciana* and *A. fatua* were susceptible or resistant to all four grass rusts. Since all wild oat seedlings exhibited susceptible infection types after inoculation with strains of oat stem rust, it is apparent that genotypes like Al and WOA can act as mutual hosts to *P. graminis avenae* and the three related grass rusts (Table 5) thus serving as a possible medium for somatic hybridization between these *formae speciales* of *P. graminis*.

Discussion

Barberry bushes (*Berberis vulgaris* L.), on which the sexual stage of oat stem rust occurs, are rarely found in eastern Australia, and examination of occasional aeciospore formation has so far failed to indicate the presence of *P. graminis avenae* on barberry in Australia. In the U.S.A. it was found that the oat stem rust pattern in the vicinity of *B. vulgaris* was more variable and hence different from that obtained from regions where barberries are absent (Roelfs and Rothman, 1971).

Luig and Watson (1970) suggested that the introduction of wheat cultivars with several different single genes for resistance has been the major factor determining variability in the Australian wheat stem rust flora. The cultivation of commercial types with complex resistances resulted in a rapid increase of strains possessing several virulence genes. Most of the variability found in *P. graminis avenae* in eastern Australia cannot be explained by the presence of resistant cultivars. The acreages in N.S.W. sown to Burke and Laggan, both with the *Pg–2* gene (Upadhyaya and Baker, 1962), Lampton with *Pg–1*, and to Garry (genes *Pg–2* and *Pg–4*), are too small to have a significant effect on the prevalence of the more virulent strains. However, it appears certain that the cultivation of Saia in Queensland has favoured the survival of strains virulent on it.

Our studies have shown that the recessive gene *pg–8* derived from C.I. 4023 (Hajira × Joanette) and present in the oat stem rust differential C.I. 8111 provides an effective source of resistance to oat stem rust in eastern Australia. Since Joanette carries gene *Pg–3* only, gene *pg–8* (F) must have come from Hajira and could be identical with one of the linked genes Hj_1 or Hj_2 found by Upadhyaya and Baker (1960) in the Hajira derivative Garry.

Virulence on *pg–8* has been found to be dominant (Martens *et al.*, 1970), and it appears that mutations from the recessive to the dominant state in the corresponding gene for virulence on *pg–8* are rare in the Australian oat stem rust flora. On the other hand, in the United States a strain virulent on this gene was identified in 1962, and increased to 70 per cent of the isolates studied in 1963 (Stewart and Roberts, 1970). To achieve a broader basis for resistance, *pg–8* should be combined with another gene, *e.g. Pg–4*, *pg–9* or *Pg–3*. However, it cannot be easily combined with *Pg–1* or *Pg–2*, since all three genes are very closely linked (McKenzie and Green, 1965).

The other factors for resistance in the seven differentials appear to be of little value on their own if incorporated into an Australian cultivar (Table 2). The factor(s) in Saia would not give effective protection in Queensland and northern N.S.W. The gene *pg–9* is recessive and, therefore, more difficult to handle in a breeding programme, and it is ineffective against several strains. Of the four dominant genes, *Pg–4* probably is of the greatest value to the breeder when combined with other resistances (Table 1). Since it is not allelic with the other designated genes of the differential set, such a task should not be difficult.

Martens *et al.* (1970) studied the gene for gene relationships in the *Avena : P. graminis* host-pathogen system in Canada. Many rust strains were found to carry factors for virulence on genes for resistance never used in North America.

Strains homozygous recessive for the genes for virulence on *Pg–1*, *Pg–2* and *Pg–4* were widespread, probably due to the cultivation of varieties with these genes. Strains with the dominant genes for virulence on *pg–8* and *pg–9* accounted also for the bulk of inoculum in western and eastern Canada respectively. Virulence on *Pg–3*, apparently controlled by an extra-chromosomal component (Green, 1965), was predominant in the rust flora in both parts of Canada. In Australia, virulence on *Pg–3* and those controlled by the recessive genes corresponding to *Pg–1*, *Pg–2* and *Pg–4* were found to be more prevalent in the rust flora than virulence conditioned on *pg–8* and *pg–9* by two single dominant genes. In this instance there appears to be no linkage in the pathogen between recessive genes for virulence and recessive deleterious genes.

Luig and Watson (1972) stated that the grass species *Agropyron scabrum* Beauv. and *Hordeum leporinum* appear to be important sources of somatic hybrids between *P. graminis* f. sp. *tritici* and *P. graminis* f. sp. *secalis*. The present study dealing with single plant progenies of wild oats suggests that hybridization might occur between oat stem rust and related grass stem rusts including *P. graminis lolii* and *P. graminis dactylidis* on certain genotypes of *A. fatua* and *A. ludoviciana*. Likewise *Dactylis glomerata* and other cultivated and native grasses comprise genotypes which are susceptible to *P. graminis avenae*, *P. graminis lolii* and to three other cultures used in this study. If somatic hybridization occurs, subsequent selection on other species could result in the establishment of different types of *P. graminis*. It has been suggested that cultures 69968 and 69243 could have arisen as somatic hybrids involving *P. graminis avenae* as one parent (Luig and Watson, 1972).

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